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Predicting effects of ship-induced changes in flow velocity on native and alien molluscs in the littoral zone of lowland rivers

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Abstract

The introduction and spread of alien mollusc species is strongly related to human activities such as connecting river basins through canal construction and shipping. Economic growth has caused an increase in commercial and recreational navigation on rivers and led to the development of extensive networks of waterways. Ships alter flow velocity in littoral zones via water displacement and propeller jet streams, thereby affecting structure and functioning of riverine mollusc communities and their ecosystem services, such as water purification and nutrient cycling. A literature review was performed to derive data for determining field based upper flow velocity occurrences for 37 native and 8 alien mollusc species present in the rivers Rhine and Meuse. Next, these upper flow velocities were used to construct species sensitivity distributions (SSDs) representing the species assemblages of native and alien molluscs in the littoral zone of these rivers. The SSDs were used to derive the potentially occurring fractions (POFs) of both species assemblages in groyne fields or in channels behind longitudinal training dams (LTDs), due to shipping induced changes in flow velocity conditions. POFs were calculated for various types of ships, in three river Rhine distributaries (Nederrijn: impounded; Waal and IJssel: free flowing) and the river Meuse (impounded). The SSDs of native and alien species assemblages did not differ significantly. Alien species with the lowest and highest tolerances were *Musculium transversum* (Say, 1829) and *Dreissena polymorpha* (Pallas, 1771), respectively. *Valvata cristata* Müller, 1774 and *Radix balthica* (Linnaeus, 1758) were the native species with the lowest and highest flow velocity tolerance, respectively. Freight ships were associated with the lowest POF in impounded rivers (0.76) as well as in free-flowing rivers (0.61). Shipping was associated with lower POFs in groyne fields of free-flowing rivers than those of impounded rivers. The highest POFs were found in channels behind an LTD in a free-flowing river. Shipping is associated with a shift of the mollusc species assemblage towards flow resistant species and could thereby affect ecosystem functioning and services.

Key words: bivalves, gastropods, navigation, species occurrence, species richness, species sensitivity distribution

Introduction

Over recent centuries many rivers worldwide have been regulated (Dynesius and Nilsson 1994). At the same time, ship transport on rivers has become more and more important to increasing global trade (Karatayev et al. 2007), facilitated by the construction of dams, weirs, canals, groynes and longitudinal training dams (LTDs) (Van Stokkom et al. 2005; Huthoff et al. 2013). Weirs ensure that water levels are high enough to allow shipping during periods of low discharge. Groynes have been constructed for safe discharge of ice, stabilising river banks and regulating depth and sedimentation in fairways (Admiraal et al. 1993; Huthoff et al. 2013). Recently, LTDs are alternatives to groynes and aim to maintain minimum water depths for shipping, discharge capacity and habitat diversity (Collas et al. 2018b). Habitat alterations may affect riverine biodiversity as they facilitate the dispersal of alien species: groynes and LTDs provide hard substrate formerly not present and may serve as habitat for alien species especially (Van Kessel et al. 2016; Collas et al. 2018b), while interconnecting canals to create extensive networks of waterways for shipping provide opportunities for alien species to disperse outside their native distribution range (Leuven et al. 2009).

Shipping itself may also affect biodiversity, as shipping causes vessel-induced pulse waves that cause hydrodynamic disturbances in aquatic environments particularly in littoral zones (Ten Brinke 2003; Gabel et al. 2011b). Ships have different characteristics (e.g. hull shape, size, propeller type, etc.) that determine the type of waves and flow velocities they produce (Ten Brinke 2003; Murphy et al. 2006). Species experience increases in turbidity (Garrad and Hey 1987; Osborne and Boak 1999; Erm and Soomere 2004), shear stress (Gabel et al. 2012) and flow velocity (Ten Brinke 2003). Shipping also affects biodiversity by serving as an important vector for introduction and secondary spread of alien species attached to ship hulls or in bilge- and ballast water (Ricciardi and MacIsaac 2000; Leuven et al. 2009; Hanafiah et al. 2013; Collas et al. 2018c). These alien species can outcompete and displace native species, due to their higher tolerances of environmental pressures like temperature and salinity (Clavero and Garcia-Berthou 2005; Leuven et al. 2009; Verbrugge et al. 2012; Collas et al. 2018a). Most research on the effects of shipping has focused on macrophytes (Eriksson et al. 2004; Weber et al. 2012), fish (Holland 1986; Arlinghaus et al. 2002; Wolter and Arlinghaus 2003; Wolter et al. 2004; Collas et al. 2018b; Zajicek et al. 2018) and macroinvertebrates including some mollusc species (Bishop 2007, 2008; Garcia et al. 2007; Gabel et al. 2008, 2011a, b, 2012, 2017). Gabel et al. (2011a) showed that the native gastropod *Bithynia tentaculata* (Linnaeus, 1758) exhibited lower growth rates than its alien counterpart *Physa acuta* (Draparnaud, 1805) under exposure to waves that are similar to ship-induced waves. Shipping can thus potentially affect freshwater mollusc species composition and reduce total species richness through replacement of native species by alien species, in particular in the littoral.

Freshwater molluscs are important for the functioning of aquatic ecosystems (Vaughn and Hakenkamp 2001; Gutiérrez et al. 2003; Sousa et al. 2008). They provide important regulating and supporting ecosystem services such as water purification, nutrient recycling and storage, and structural habitat (Covich 2010; Lummer et al. 2016; Vaughn 2018). However, molluscs experience increasing pressures from global change such as increases in low water level events, temperature, salinity and competition with alien species (Verbrugge et al. 2012; Leuven et al. 2009, 2014; Lopes-Lima et al. 2016; Collas et al. 2014, 2018a). Alien mollusc species with higher tolerances for some pressures (e.g. wave stress, temperature and salinity) are able to outcompete native mollusc species (Gabel et al. 2011a; Verbrugge et al. 2012; Collas et al. 2018a).

The effects of shipping-induced changes in flow velocity on native and alien mollusc assemblages in littoral zones of lowland rivers have not yet been quantified. Therefore, this study aims to assess the potential occurrence of native and alien mollusc species in relation to flow velocity and to predict the effects of changes in ship-induced flow velocities on species richness of molluscs in littoral zones (e.g. groyne fields and channels behind LTDs) of lowland rivers. Moreover, the implications of these shipping effects on mollusc' provisioning of ecosystem services is discussed.

Materials and methods

Species selection and flow velocity sensitivity

A complete and up-to-date list of native and alien freshwater molluscs occurring in the lowland sections of the rivers Rhine and Meuse in the Netherlands was compiled using Gittenberger et al. (2004), Leuven et al. (2009), Verbrugge et al. (2012), Matthews et al. (2014), and Collas et al. (2017, 2018a, c). Data on the occurrence of freshwater bivalves and gastropods in relation to water flow velocity was acquired from the database of Collas et al. (2018a) and a Google scholar literature search, respectively. The search terms were "scientific species name" combined with "flow velocity". The final dataset consisted of 1344 global presence/absence entries. Only data for which flow velocity was measured at the same sampling site and date as where a species was found was retained for analyses resulting in 700 entries for 45 mollusc species. Using this dataset the minimum and maximum flow velocities of occurrence were obtained for each species (Supplementary material Table S1).

Species sensitivity distributions

The relationship between the potentially occurring fraction (POF) of a species assemblage and the presence of an environmental pressure can be derived from a species sensitivity distribution (SSD) (Posthuma et al. 2002; Smit et al. 2008; Leuven et al. 2011; Verbrugge et al. 2012; Collas et al. 2014, 2018a; Del Signore et al. 2016). In the present research the POF represents the fraction of the mollusc species assemblage that can potentially occur at specific flow velocities. For example, a flow velocity that results in a predicted POF of 0.6, indicates that 60% of the mollusc species assemblage is tolerant of these flow conditions, and therefore potentially able to occur.

Data on occurrence of molluscs at maximum flow velocities was divided into two sets and used to derive SSDs for 1) native molluscs and 2) alien molluscs. The mean and standard deviation of the distribution depict the average and variation in tolerance of species, respectively. The normality of the alien and native data sets was checked using the “shapiro.test()” function in R (R Core Team 2015) and both met the requirement of normality. As a result normal distributions were fitted to the alien and native data set, as well as a combined data set of all mollusc species, using the fitdistrplus package in R-statistics (R Core Team 2015; Delignette-Muller and Dutang 2015; Szöcs 2015). The fitted normal distributions represent the SSDs for the mollusc assemblages (Figures 2 and 3). To determine the reliability of the fitted distributions, the 2.5% and 97.5% confidence intervals (CI) were derived for the distributions and their means and standard deviations using a bootstrapping function with a thousand iterations in R (R Core Team 2015).

To elucidate whether maximum flow velocity sensitivities differed between alien and native molluscs, the maximum flow velocities under which both species groups occurred were compared using an independent sample t-test in R (R Core Team 2015). An independent test was used since the occurrence data originated from different locations. Additionally, to determine the power of the comparison between alien and native mollusc sensitivity to flow velocity a power analysis for the t-test was performed using the pwr package in R (R Core Team 2015). Based on significant differences between native and alien mollusc regarding other environmental variables (e.g. temperature and salinity, Verbrugge et al. 2012) a large effect was expected, so effect size was set at 0.8 as this is considered a large effect by Cohen (1998), and α was 0.05. To determine if variability in maximum flow velocity sensitivity differed between alien and native mollusc assemblages a Levene’s test was performed using the “levene’s.test()” function in R (R Core Team 2015).

Littoral exposure per type of ship

To determine the ship-induced exposure of the microhabitats within groyne fields and behind LTDs to flow velocity, measurements were conducted at three different sites in the intensively navigated rivers Rhine and Meuse. The river Rhine splits into three distributaries in the Netherlands, the rivers Waal, Nederrijn and IJssel. The rivers Nederrijn and Meuse are impounded and the rivers Waal and IJssel are free flowing (Nienhuis et al. 2002; Leuven et al. 2014). The changes in flow velocity ($cm \cdot s^{-1}$) caused by single passing ships were measured using a TAD-micro flow velocity meter (probe: W16, Höntzsch GmbH-W, Germany) and two open channel flow meters (Valeport, model 002; Flow Rate Sensor, Vernier). These flow velocity data were used to determine the maximum velocity (V_{max}) produced per ship type (by taking the highest flow velocity, see Figure 1). We chose maximum velocity over mean velocity, as the mean velocity is not representative of the hydrologic disturbance occurring with passing ships. Ships create waves that have strong amplitudes and short peaks of relatively high flow velocity (Figure 1; Bhowmik and Mazumder 1990; Rodriguez et al. 2002), which can be strong enough to detach molluscs (Gabel et al. 2008, 2012). Therefore, maximum velocity is expected to be a better indicator of hydrological disturbance. Vessel type for each ship was determined from the MarineTraffic (2018) database and subsequently categorizing as: recreational ship; container ship; river cruise ship; tanker; freight ship; towboat with no barge and service ship. The acquired V_{max} of each ship type were entered into the distribution of the combined (all species) SSD to derive the corresponding POFs of the mollusc assemblage associated with different ship types and in different habitats.

Results

Species flow velocity sensitivity

Field data on the occurrence of molluscs in relation to flow velocity was available for eight currently present

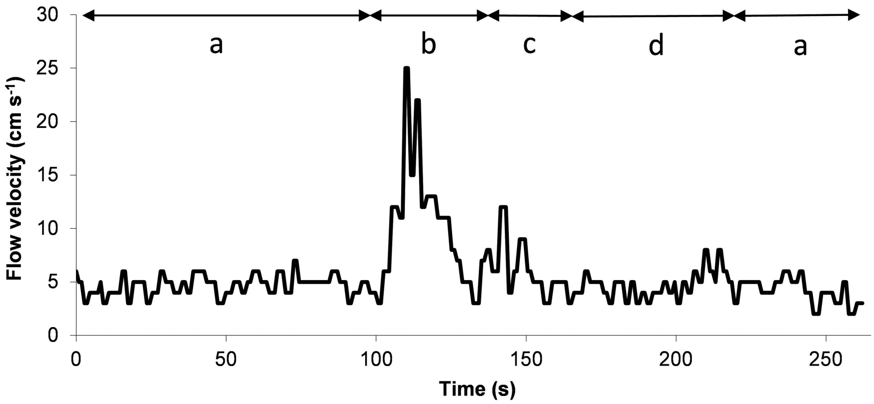

Figure 1. The changes in flow velocity within a microhabitat located in a groyne field, produced by a freight ship navigating on the Nederrijn River at Lexkesveer (51°57′34.1″N; 5°41′17.0″E), April 11, 2012 (a: reference flow; b: water displacement flows; c: bow and propeller waves; d: secondary waves).

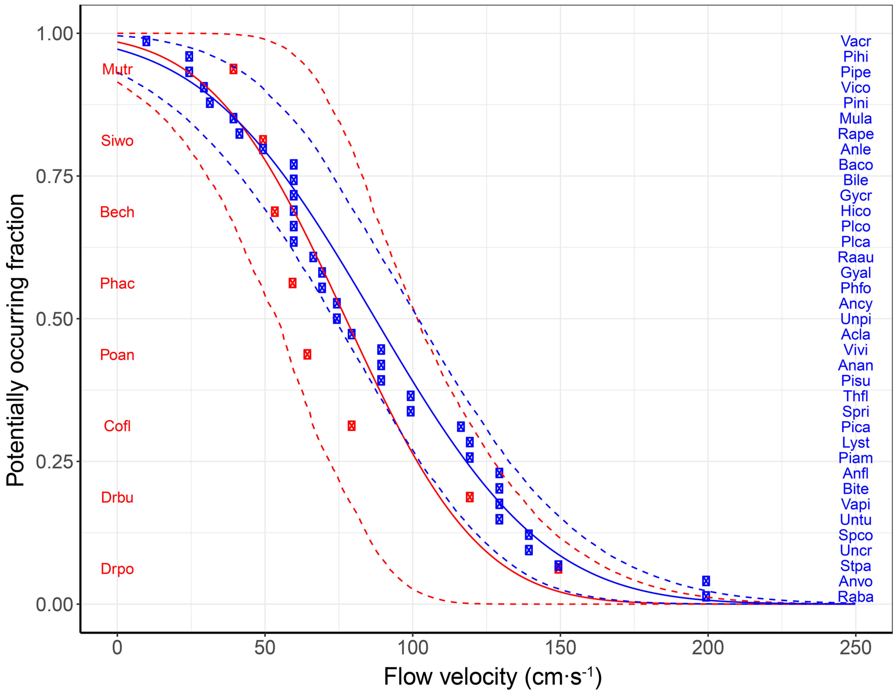

Figure 2. The field based species sensitivity distribution and the 2.5 and 97.5% confidence intervals for occurrence of alien molluscs (red; n = 8; mean = 77.4 cm·s^{-1} and sd = 35.8 cm·s^{-1}) and native molluscs (blue; n = 37; mean = 87.3 cm·s^{-1}, standard deviation = 45.6 cm·s^{-1}) in relation to flow velocity in their habitat. The data points represent the maximum recorded field occurrence of species. For each data point the according species abbreviation is listed, abbreviations can be found in Table S1.

alien species and 37 native species occurring in the Rhine-Meuse river delta (Table S1). The range of occurrences at maximum flow velocities for alien species was between 40 and 150 cm·s^{-1} for *Musculium transversum* (Say, 1829) and *Dreissena polymorpha* (Pallas, 1771), respectively; for native species between 10.5 and 200 cm·s^{-1} for *Valvata cristata* Müller, 1774 and *Radix balthica* (Linnaeus 1758), respectively (Table S1).

Species sensitivity distributions (SSDs)

Means and standard deviations of both SSDs were not significantly different (Student t-test: t = 0.64, p = 0.53; Levene's test: F = 0.77, Df = 1, p = 0.38). The mean of the SSD for alien and native species was 77.4 (CI: 54.1–101.6) and 87.3 (CI: 73.4–101.9) cm·s^{-1}, respectively (Figure 2). The standard deviation of the SSDs was 35.8 (CI: 15.7–50.4) for alien and 45.6 (CI: 34.5–54.7) cm·s^{-1} for native molluscs. The overall SSD had a mean of 85.6 (CI: 72.3–98.8) cm·s^{-1} and a standard deviation of 44.2 (CI: 34.7–52.4) cm·s^{-1} (Figure 3).

Exposure per ship type

Ships cause changes in flow velocity within microhabitats located in littoral zones (Figure 1). For all three different microhabitats the highest V_{max} was due to the passing of freight ships (54.0, 73.7 and 25.7 cm·s^{-1}, respectively; Table 1). The potentially occurring fraction (POF) was reduced to 61% during

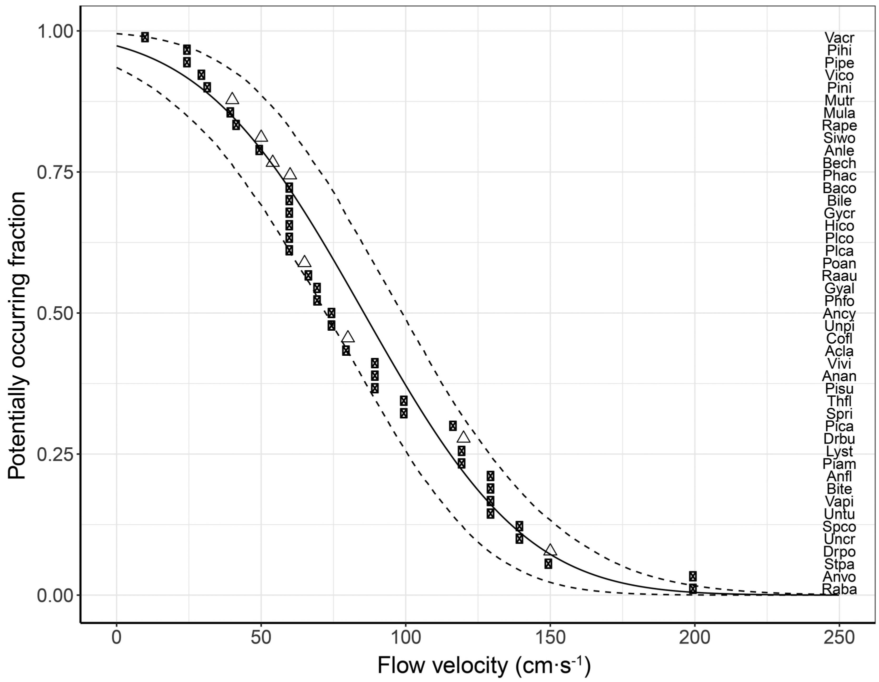

Figure 3. The field based species sensitivity distribution and the 2.5 and 97.5% confidence intervals for occurrence of freshwater molluscs (n = 45; mean = 85.6 cm·s^{-1} and sd = 44.2 cm·s^{-1}) in relation to flow velocity in their habitat. The data points represent the maximum recorded field occurrence of species, triangles represent alien species and squares represent native species. For each data point the according species abbreviation is listed, abbreviations can be found in Table S1.

Table 1. Maximum flow velocity (V_{max}) in the littoral zones of groyne fields and side channels along longitudinal training dams caused by water displacement flows of various types of passing ships and corresponding potentially occurring fraction (POF) of sessile mollusc species derived from their species sensitivity distribution (Figure 2).

Ship type	Vmax (cm·s^{-1})						Potentially occurring fraction		
	Groyne field in impounded river	N	Groyne field in free-flowing river	N	Free-flowing side channel along LTD*	N	Groyne field in impounded river	Groyne field in free-flowing river	Free-flowing side channel along LTD*
Recreational ship	30.0	8	19.6	6	n.a.	n.a.	0.90	0.93	n.a.
Container ship	18.0	1	43.4	11	16.5	2	0.94	0.83	0.94
River cruise ship	21.0	2	10.2	2	23.2	2	0.93	0.96	0.92
Tanker	11.0	2	49.2	98	25.6	13	0.95	0.79	0.91
Freight ship	54.0	43	73.7	166	25.7	23	0.76	0.61	0.91
Towboat no barge	39.0	1	61.1	6	n.a.	n.a.	0.85	0.71	n.a.
Service ship	47.0	4	45.1	32	15.6	1	0.81	0.82	0.94

* LTD: longitudinal training dam; n.a.: not available

the passage of freight ships in the free flowing rivers. Average POF associated with various types of ships was 88% and 81% for impounded and free-flowing rivers, respectively. Behind the LTD in the free-flowing river the POF was the highest at 94%.

Discussion

Field based tolerance data

The data for the species specific sensitivity distributions was based on global field measurements because of a lack of sufficient and consistent experimental data on the tolerance of mollusc species to flow velocities. Many experimental studies focus on dislodgement of species exposed to continuous flow velocities (Dorier and Vaillant 1954; Moore 1964; Dussart 1987; Peyer et al. 2009). Although the results of these studies are valuable, the difference in experimental set-up (e.g. flume type, exposure duration, species acclimation) can complicate comparisons. Moreover, molluscs can also experience other processes under high flow, such as reduction in breathing capacity, movement and clearance capacity (Statzner and Holm 1989; Ackerman 1999). Comparison of experimental data on flow tolerance with field occurrence based data shows experimentally derived tolerances to flow velocity may be higher as well as lower than field based values (Table S2). However, caution is needed when comparing these data types due to differences in experimental set-up and end-points for flow tolerance. Experimental laminar flows can result in drag effects while field data provide a more realistic display of the ambient (flow-induced) environmental conditions experienced by molluscs, since flow can be multidirectional and induce other flow velocity effects (e.g. increase in turbidity). Our analyses are dependent on global field data availability. To reduce this dependency and get a more consistent threshold for flow velocity tolerance, a generalized linear model (GLM) with a binomial (absence/presence) distribution could be applied. However, our database was focused on species presence at flow velocities and included only limited absence data. Determining species absence under certain conditions is inherently biased by sampling efforts and sampling times (Gu and Swihart 2004). In contrast, using species presence data ensures that the species is able to cope with the flow conditions, thereby increasing the reliability of our effect level. At most the effect level might be over- or underestimated due to variability in flow velocity measurement protocols but this would also hold for absence data. In addition, Verbrugge et al. (2012) also used field occurrence in relation to maximum temperature and salinity for constructing SSDs. Thus, the occurrence of species in relation to maximum flow velocity in the field was regarded as a good performance indicator for its sensitivity to changes in flow velocity by ships.

Species Sensitivity distributions (SSDs)

There has been some critique on the use of SSDs due to their assumptions. First, it is assumed that the distribution in species sensitivity in natural ecosystem approximates the theoretical distribution. To reduce the chance of a large discrepancy between the SSD and the natural situation, it is important to include as many species as possible to improve the reliability of the SSD. Due to the lack of a significant difference and the low number of alien species, we combined alien and native data into one dataset to improve the reliability of the SSD (Del Signore et al. 2016). Second, the species used in the SSD provide an unbiased measure of the variance and mean sensitivity distribution of species in natural ecosystems (Forbes and Forbes 1993). This assumption mostly forms a limitation when using several taxa, as sensitivity towards a certain (toxicological) pressure can differ between taxa. Here, the focus on a single species group (molluscs) reduces inter-species group differences in sensitivity (Del Signore et al. 2016). With regard to ecological relevance of SSDs there are two more assumptions: by protecting species community composition the community function is also protected; and species interactions can be ignored (Forbes and Forbes 1993). We acknowledge the limitations produced by these two assumptions. However, we consider the use of SSDs to provide a first insight on potential effects of environmental pressures. After initial assessment using SSDs further research can be directed towards quantifying effects on community function and including species interactions. SSDs have been widely accepted in the scientific literature for predicting species community effects under certain environmental pressures (e.g. Kefford et al. 2006; Piscart et al. 2011; Collas et al. 2014, 2018a; Del Signore et al. 2016). Hence, the use of an SSD to predict effects of shipping on mollusc communities was valid.

There are no overall differences in sensitivity to maximum flow velocity between alien and native mollusc species assemblages. This contrasts results found for other environmental pressures where alien species were found to have higher tolerances towards temperature and salinity (Verbrugge et al. 2012; Collas et al. 2018a), but is concordant with the results found for air exposure, dissolved oxygen levels and water depth (Collas et al. 2014, 2018a). The power analysis yielded a power of 0.52 which indicated that our sample size of alien species might have been too small, increasing the likelihood of a type II error. However, future introductions of alien species will increase the total number of alien species within the mollusc communities of the Rhine-Meuse river delta and might result in statistical significant differences in sensitivity to maximum flow velocity between alien and native mollusc species assemblages. Another possible explanation for the absence of differences in sensitivity to flow velocity is that water flow—unlike, for example, temperature—is much less dependent on geographical latitude and longitude of the natural range of riverine species but predominantly determined by the bed slopes and discharge regimes of rivers in their native ranges (Schulze et al. 2005).

The combined SSD was used for predicting the molluscs occurring in littoral zones of the rivers Rhine and Meuse. The highest tolerances were found for the gastropods *R. balthica* and *Anisus vortex* (Linnaeus, 1758). For the bivalves, *D. polymorpha* had the highest flow velocity tolerance. In contrast to the two gastropods, *D. polymorpha* is a sessile species that attaches to substrate using byssus threads (Grutters et al. 2012), which allow *D. polymorpha* to resist high flow velocities. Possible explanations for the relatively high tolerance of *R. balthica* and *A. vortex* might be the attachment force of their foot or a behavioural strategy. *Radix balthica* is a broad-footed species and a solid substratum helps snails to maintain their hold in fast flowing water (Hynes 1970). Some snails are able to adjust the angle and position of their shell and body to cope with increasing flow velocities (Moore 1964; Dussart 1987; Statzner and Holm 1989) or produce mucus to adhere to the surface (Moore 1964; Schnauder et al. 2010). Although there was no difference in sensitivity to maximum flow velocity between native and alien mollusc species, our data is useful for creating additional SSDs based on other species' traits.

Ship-induced flow velocities

Different types of ships produce waves of different strengths, depending on factors like speed, and hull and propeller characteristics (Murphy et al. 2006; Gabel et al. 2017), which need to be taken into account with respect to effects of ship-induced flow velocity. During our field survey, changes in flow velocities and maximum velocities (V_{max}) produced by numerous ships of different types were measured in three littoral habitat types: 1) groyne fields in a free flowing river, 2) groyne fields in impounded rivers, and 3) side channel behind an LTD in a free flowing river. The maximum flow velocities caused by most ships were higher than the natural maximum flow velocities occurring in the three littoral habitat types, which ranged from 13.0 to 13.6 $cm \cdot s^{-1}$.

The determined POFs in the habitats are predictions and it is apparent that additional field surveys on mollusc species abundance in these different habitats are needed to validate these predictions. However, field surveys are costly and time consuming compared to SSD's, which allow a relatively fast and cheap first assessment of the potential effects of shipping on the mollusc species community.

The lowest increase in flow velocity for several ships was found in the habitats behind the LTDs in the free flowing river (river Waal) showing that the highest POF of the mollusc species assemblage can occur in these habitats. This agrees with Collas et al. (2018b) who showed that LTDs mitigate the effects of shipping on environmental conditions and facilitate higher fish densities than traditional groyne fields. The lowest POF for molluscs (0.61) was associated with a freight ship in a groyne field located in a free flowing river. This type of ship has the potential to suppress 39% of the potential mollusc species assemblage (Table 1). This could imply that shipping could cause a shift in the mollusc species assemblage towards more flow tolerant species.

We only measured flow velocities in the littoral habitat and could not determine the ship induced flow velocities in deeper waters i.e. the main channel. Perhaps species are less affected by ship-induced flow velocities in deeper waters and could use these habitats as refugia (Miller et al. 1999; Gabel et al. 2017). However, environmental conditions in deeper waters can also differ from littoral habitats (e.g. temperature, substrate; Matthews et al. 1994; Beckmann et al. 2004; Bij de Vaate et al. 2007; Webb et al. 2008) which could impede species finding refuge in the deeper waters. Next steps should be performing flow velocity measurements in deeper waters and field surveys in the aforementioned habitats and deeper waters to validate the prediction of a shift in the mollusc species assemblage and potential species' survival in deeper waters. Moreover, these field surveys should also monitor whether (new) alien species have settled and, if so, to what extent. Validating these predictions and monitoring is important because both gastropods and bivalves provide important ecological functions and services.

Implications for ecosystem services

Shipping affects the ecosystem services of molluscs. A direct effect is the suppression of mostly gastropod species that provide ecosystem services such as nutrient recycling and are an important part of food webs that transfer energy to higher trophic levels (Covich 2010). Some gastropods are also able to provide water purification services through biofiltration (Brendelberger and Jürgens 1993). However, their filtration rates are low compared to the filtration rates of bivalve species (Kryger and Riisgård 1988). The bivalve filtration rates are directly affected by shipping-induced shear stress (Lorenz et al. 2013). Although we found no differences in sensitivity to flow velocity between native and alien molluscs, the filtration rates of two alien bivalves, *Dreissena rostriformis bugensis* Andrusov, 1897 and *Corbicula fluminea* (Müller, 1774), were less affected by wave disturbance conditions than that of native unionid and sphaeriid bivalves (Lorenz and Pusch 2013). Thus, shipping can potentially cause differences in performance between native and alien bivalves and thereby directly affect bivalves' ecosystem services provisioning. A potential indirect effect is shipping mediated dispersal and establishment of alien invasive species (Leuven et al. 2009). Bivalve species such as *D. polymorpha*, *D. rostriformis bugensis* and *C. fluminea* have established themselves in European rivers (Matthews et al. 2014) and are outcompeting native bivalves such as *Unio pictorum* (Linnaeus, 1758) and *Unio tumidus* Philipson, 1788 (Leuven et al. 2014), through fouling their shells and depleting food sources (Strayer 1999). The exclusion of native bivalves by alien bivalves could potentially affect the ecosystem services provisioning of the bivalve community. The individual filtration rates of alien bivalves were lower than the rates of native bivalves. This is likely due to the larger sizes of the native unionids, as filtration rates per gill area unit are more similar in range (Kryger and Riisgård 1988; Diggins 2001). Alien bivalves often form relatively dense assemblages (Kryger and Riisgård 1988; Leuven et al. 2014) which should allow the bio-filtration capacity of the newly formed alien and native mussel assemblage to remain stable, or potentially even increase at high mussel densities. Thus, the establishment of alien species does not necessarily have to deteriorate the water purification capacity of the mollusc species assemblage. On the contrary, some alien species have the potential to improve this capacity. So, from an ecosystem services perspective, an increase in alien species abundance might be beneficial, depending on which species will establish. However, from a biodiversity perspective this increase can be detrimental as different species assemblages are homogenised and biodiversity may decline (Mckinney and Lockwood 1999).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Overview of minimum and maximum flow velocities at which native and alien benthic molluscs were observed in the field.

Table S2. A comparison between field based and experimental based data of tolerance to flow velocity.

Appendix 1. Supplementary references.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Koopman_etal_SupplementaryTables.xlsx